

Long-term effects of scrub clearance and litter removal on the re-establishment of dry alvar grassland species

Jan P. Bakker^{1,*}, Eje Rosén^{2,3}, Wim A. Ozinga^{4,5}, Mario Bretfeld⁶,
Tobias Feldt⁶ & Julia Stahl⁶

¹ Community and Conservation Ecology, University of Groningen, P.O. Box 11103, NL-9700 CC Groningen, The Netherlands (*corresponding author's email: j.p.bakker@rug.nl)

² Department of Plant Ecology, EBC, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden

³ Station Linné, Ölands Skogsby 161, SE-386 93 Färjestaden, Sweden

⁴ Alterra Wageningen University & Research, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands

⁵ Department of Ecology, Radboud University Nijmegen, Toernooiveld 1, NL-6525 ED Nijmegen, The Netherlands

⁶ Landscape Ecology Group, Carl von Ossietzky University Oldenburg, D-26111 Oldenburg, Germany

Received 27 July 2011, final version received 13 Oct. 2011, accepted 27 Oct. 2011

Bakker, J. P., Rosén, E., Ozinga, W. A., Bretfeld, M., Feldt, T. & Stahl, J. 2012: Long-term effects of scrub clearance and litter removal on the re-establishment of dry alvar grassland species. — *Ann. Bot. Fennici* 49: 21–30.

Many characteristic dry alvar grassland species disappear after cessation of livestock grazing as a result of encroachment by *Juniperus communis*. We studied the re-establishment of these species after scrub clearance with and without the removal of the layer of litter and mosses in long-term (14 years) permanent plots. Most of the species belonging to the community species pool of dry alvar grassland species before clearance were found in permanent plots between 2 and 14 years after the clearance. A large part originated from vegetative spread of already occurring species in the established vegetation in the surroundings. Only a small part of the long-term persistent soil seed bank resulted in the re-establishment of alvar species. There was no significant difference in the traits soil seed bank, seed weight and long-distance dispersal by wind, dung or fur of animals of established and non-established species. Removal of litter and mosses positively affected the re-establishment of alvar species.

Introduction

The dry alvar grasslands in Estonia (Pärtel *et al.* 1999), in Russia (Znamenskiy *et al.* 2006), in Canada (Schaefer & Larson 1997) and on the Baltic islands of Gotland and Öland (Sweden) feature very species-rich limestone plant com-

munities with approximately 80 species/100 m² and 40 species/m² (Van der Maarel & Sykes 1993). Alvar refers to dry grassland plant communities growing on thin soil (up to 20 cm, but can locally be deeper) over limestone bedrock (Königsson 1968, Rosén 1982). The alvar has never been fertilized and has only been exploited

for cattle, sheep and horse grazing and firewood collection and is, therefore, of great nature conservation interest (Rosén & Van der Maarel 2000).

The degree of scrub encroachment differs between areas. In Russia, the small alvars have not been overgrown with scrub, although they are not grazed (Znamenskiy *et al.* 2006). In Canada, alvars were burnt in the past. Abandonment after burning does sometimes result in scrub formation (Schaefer & Larson 1997). However in Estonia, the majority of alvars have been abandoned and got either overgrown or were deliberately planted with *Pinus sylvestris* (Pärtel *et al.* 1998). In Sweden, the vegetation harbours the species-rich *Veronica spicata*–*Avenula pratensis* association (Bengtsson *et al.* 1988). The association includes individuals of *Juniperus communis*, which develop to form juniper shrubland after the cessation of grazing and firewood collection (Rosén 1988).

This process of scrub encroachment is accompanied by a decrease in species richness, including the disappearance of characteristic alvar species. The number of alvar species in the established vegetation declines continuously with an increasing cover percentage of junipers. This drop in species numbers is dramatic when the shrub cover reaches between 75% and 100%, causing subsequent light attenuation (Rejmánek & Rosén 1988, 1992). However, part of the alvar species can survive in the long-term persistent soil seed bank. The decline in numbers of viable alvar species in the soil seed bank is more pronounced, the longer ago the scrub encroachment by junipers started (Bakker *et al.* 1996). A decline of calcareous grassland species in the soil seed bank after abandonment and subsequent *Pinus sylvestris* encroachment in Germany was also found by Poschlod *et al.* (2002). In contrast, after 40 years of establishment of *Pinus sylvestris* no decline in species number was found in the established vegetation or soil seed bank in the alvar communities in Estonia (Kalamees & Zobel (1997).

A high percentage of juniper cover coincides with a dense layer of litter, lower soil pH, low vascular plant survival and thickness of the moss carpet as a result of changing microclimate

(Rosén 1982, Rosén & Sjögren 1988). Mosses may form a barrier for seeds to reach the soil as shown in introduction experiments in a range of ecosystems such as dry grasslands (Van Tooren 1990, Jeschke & Kiehl 2008), flood meadows (Hölzel 2005) and moist fen meadows (Stammel *et al.* 2006). In addition, a field experiment adding litter on fen meadows revealed that seedling establishment of fen meadow species was significantly hampered by litter (Jensen & Gutekunst 2003)

The present study focuses on the re-establishment of the original dry alvar grassland species after cutting of junipers, and removal of the litter and moss layer in a partly overgrown area on the Baltic island of Öland. We hypothesize that (i) only a part of the characteristic species can emerge, namely those having a long-term persistent soil seed bank, and (ii) removal of the litter and moss layer has a positive effect on species emergence. Apart from the species traits persistent or transient seed bank, we took into account the dispersal traits of seed weight and dispersal by animals and wind. Small seeds tend to be persistent (Pakeman *et al.* 2002). Species with a transient seed bank need a mechanism for long-distance dispersal to re-establish in restored sites.

Methods

Study site

The study site is located in the northern part of the large alvar area 'Stora Alvaret' on the southern half of the Baltic island of Öland, SE Sweden, ca. 0.5 km NE from the abandoned hamlet of Dröstorp at 56°35'N, 16°34'E. A dense juniper scrub of about 7 ha established itself 80 years after abandonment, whereas livestock grazing continued on the surrounding alvar. Narrow tracks and droppings of cattle, roe deer (*Capreolus capreolus*) and hares (*Lepus europaeus*) indicated some grazing inside the juniper scrub. However, gradually the tracks became overgrown, and we found no droppings of large herbivores. Hence, we assumed that the experimental plots were not grazed after clear-

ance. Locally, the junipers were tall (up to 3 m), and their cover was up to 90%. The thickness of the soil was about 20 cm, which is in the range of the characteristic alvar community of *Veronica spicata*–*Avenula pratensis*. This community was found in the cattle-grazed area around the scrub.

We sampled the soil seed bank under the dense junipers in April 1994 (Bakker *et al.* 1996) and found 36 alvar species in the established vegetation in ten 2×2 m plots (40 m²), and 30 in the soil seed bank, 13 of which were not present in the established vegetation (Bakker *et al.* 1996). Hence, the community pool (Zobel *et al.* 1998) of alvar species under the junipers amounted to 49 species in 1994 (Table 1). Two of the ten 2×2 m plots were adjacent to the areas of 50 m² where we cut the junipers in April 1994. The clearings were surrounded by a dense juniper scrub. In each clearing of 50 m² we removed litter from 25 m². This allowed for a comparison between a situation in which the thick layer of mosses and litter remained (four permanent plots) *versus* a situation in which it was removed (four permanent plots). Litter and mosses were removed by manual raking in order to expose the soil seed bank to full light and remove mechanical barriers for seedling establishment.

Vegetation sampling

The eight permanent plots (2×2 m) were monitored from 1994 to 1999, in 2003, 2004 and in 2008 during the 14-year period 1994–2008. For all the years the presence/absence of plant species was recorded. For 2008, we estimated the cover of individual species according to the decimal scale (Londo 1976). Nomenclature of species followed Lid (1987). The species were assigned to the following categories: dry alvar species (A), woodland species (W), species of depressions (D), and species of habitats strongly affected by man (M) according to Van der Maarel (1988) and Rejmánek and Rosén (1988) (*see also* Bakker *et al.* 1996, 2007).

Monitoring of the permanent plots included cutting of resprouting tall saplings of *Rosa canina* and *Prunus spinosa* (following cover estimates for these two species) in order to allow

recording of the understorey species. *Juniperus communis* did not resprout.

Dispersal traits

Several traits relevant for dispersal in time (soil seed bank) or dispersal in space (long-distance dispersal; LDD) were compared for the 48 established and the 11 non-established species. Trait data were derived from the LEDA traitbase with life-history traits of species of the northwestern European flora (Knevel *et al.* 2003, Kleyer *et al.* 2008), and adapted to a binary classification (Ozinga *et al.* 2004, 2009). We considered persistence in the soil seed bank, seed weight, and capacity for dispersal by the following vectors, all capable of providing effective long-distance dispersal (> 100 metres): dung of large mammals, fur of large mammals and wind (Table 1).

Data analysis

Differences in cover percentage between species categories as well as differences between the two litter treatments were tested using univariate general linear models based on the four replicates. The representation of dispersal syndromes for established *versus* non-established species was tested using a logistic regression analysis.

Results

Vegetation 14 years after clearing

Fourteen years after clearing, the coverage of alvar species (e.g. *Filipendula vulgaris*, *Fragaria viridis*, *Phleum phleoides*) amounted to 90% in the plots with litter removed and 55% in the plots with litter. The accumulated coverage of woodland species (mostly *Prunus spinosa*, *Berberis vulgaris*, *Cotoneaster integerrimus*, *Fragaria vesca*) amounted to 90% in both treatments. While the differences in vegetation cover between the species categories were highly significant, with woodland and alvar species having the highest cover and depression, and

Table 1. Occurrence of alvar grassland species in the established vegetation and the soil seed bank (both forming the species pool of 49 alvar species) in the dense junipers after 80 years of abandonment in 1994 (derived from Bakker *et al.* 1996), and occurrence of alvar grassland species in the vegetation in the plots cleared in April 1994. Species occurrence is given for the two treatments one year (1995) and 14 years (2008) after clearing (1, 2, 3, 4 means the species is found in one, two, three or four replicates, respectively). For each species information is given on persistence in the soil seed bank (1 = short term or long-term persistent), mean seed weight (mg), and capacity for long-distance dispersal (LDD) by dung, fur, or wind (1 = high capacity).

| Species | 80 years abandoned | | | Cleared in 1994 | | | Species traits | | | | | |
|-----------------------------------|------------------------|-----------|---|-----------------|----------------|--------|----------------|---------------------------|------------------|------|-----|------|
| | Established vegetation | Seed bank | + | 1995 | | 2008 | | Persistent soil seed bank | Seed weight (mg) | LDD | | |
| | | | | Litter | Litter removed | Litter | Litter removed | | | dung | fur | wind |
| <i>Agrostis capillaris</i> | + | + | 4 | 3 | 3 | 4 | 1 | 0.07 | 0 | 0 | 0 | 0 |
| <i>Avena pratensis</i> | + | + | 3 | 2 | 3 | 3 | 0 | 1.78 | 1 | 1 | 1 | 0 |
| <i>Briza media</i> | + | + | 1 | 2 | 1 | 1 | 1 | 0.27 | 0 | 0 | 0 | 0 |
| <i>Campanula persicifolia</i> | + | + | 4 | 4 | 4 | 4 | 1 | 0.07 | 0 | 0 | 0 | 0 |
| <i>Campanula rotundifolia</i> | + | + | 4 | 4 | 2 | 4 | 1 | 0.06 | 0 | 0 | 0 | 0 |
| <i>Carex caryophylla</i> | + | + | 2 | 2 | — | — | 1 | 0.72 | 0 | 0 | 0 | 0 |
| <i>Carex ericetorum</i> | + | + | 2 | — | — | — | 1 | 0.8 | 0 | 0 | 0 | 0 |
| <i>Cerastium fontanum</i> | + | + | 1 | 4 | 1 | — | 1 | 0.1 | 1 | 0 | 0 | 0 |
| <i>Hieracium pilosella</i> | + | + | 3 | 3 | 2 | 2 | 0 | 0.15 | 0 | 0 | 0 | 1 |
| <i>Hypericum perforatum</i> | + | + | 1 | 3 | 2 | 3 | 1 | 0.08 | 0 | 0 | 0 | 0 |
| <i>Luzula campestris</i> | + | + | 2 | 4 | 1 | — | 1 | 0.95 | 0 | 0 | 0 | 0 |
| <i>Poa angustifolia</i> | + | + | 4 | 3 | 3 | 4 | 1 | 0.019 | 1 | 1 | 1 | 0 |
| <i>Poa compressa</i> | + | + | — | — | — | — | 1 | 0.21 | 1 | 1 | 1 | 0 |
| <i>Potentilla tabernaemontani</i> | + | + | 3 | 4 | 1 | 3 | 1 | 0.71 | 1 | 0 | 0 | 0 |
| <i>Stellaria graminea</i> | + | + | 3 | 2 | 2 | — | 0 | 0.37 | 1 | 0 | 0 | 0 |
| <i>Taraxacum</i> spp. | + | + | 4 | 4 | — | — | 1 | 0.78 | 1 | 1 | 1 | 1 |
| <i>Veronica spicata</i> | + | + | 1 | — | — | — | 1 | 0.9 | 1 | 1 | 0 | 0 |
| <i>Agrostis vinealis</i> | + | — | — | — | — | — | 1 | 0.06 | 1 | 1 | 1 | 0 |
| <i>Asperula tinctoria</i> | + | — | 4 | 3 | 2 | 1 | 0 | 0.65 | 1 | 1 | 1 | 0 |
| <i>Avena pubescens</i> | + | — | 2 | 2 | 2 | 2 | 0 | 1.93 | 0 | 1 | 0 | 0 |
| <i>Danthonia decumbens</i> | + | — | — | — | — | — | 0 | 0.8 | 1 | 0 | 0 | 0 |
| <i>Draba incana</i> | + | — | — | — | — | — | 0 | 0.12 | 0 | 0 | 0 | 0 |
| <i>Festuca ovina</i> | + | — | 4 | 2 | 4 | 4 | 1 | 0.5 | 1 | 1 | 1 | 0 |
| <i>Filipendula vulgaris</i> | + | — | 4 | 4 | 4 | 4 | 0 | 1.03 | 0 | 1 | 1 | 0 |
| <i>Fragaria viridis</i> | + | — | 4 | 4 | 4 | 4 | 0 | 0.35 | 0 | 0 | 0 | 0 |
| <i>Galium boreale</i> | + | — | 2 | 2 | 2 | 2 | 0 | 0.59 | 0 | 0 | 1 | 0 |
| <i>Galium verum</i> | + | — | 1 | 4 | 4 | 3 | 0 | 0.24 | 1 | 0 | 0 | 0 |

| | | | | | | | | | | | | |
|---------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|---|---|---|---|---|---|
| <i>Knautia anvensis</i> | + | - | 1 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Orchis mascula</i> | + | - | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Phleum phleoides</i> | + | - | 2 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| <i>Primula veris</i> | + | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Prunella grandiflora</i> | + | - | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Prunella vulgaris</i> | + | - | - | - | - | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| <i>Trifolium montanum</i> | + | - | - | - | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Trifolium pratense</i> | + | - | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Vicia cracca</i> | + | - | - | - | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Anthyllis vulneraria</i> | - | + | 3 | 4 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Arenaria serpyllifolia</i> | - | + | 3 | 4 | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Centaura scabiosa</i> | - | + | - | - | - | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| <i>Erigeron canadense</i> | - | + | - | - | - | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| <i>Linum catharticum</i> | - | + | 1 | 1 | - | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Lotus corniculatus</i> | - | + | 2 | 3 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Oxytropis campestris</i> | - | + | - | - | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Polygala vulgaris</i> | - | + | 4 | 4 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Sedum acre</i> | - | + | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Sedum reflexum</i> | - | + | - | - | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Trifolium campestre</i> | - | + | 2 | 3 | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Trifolium repens</i> | - | + | 4 | 4 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Viola rupestris</i> | - | + | - | 1 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Arabis hirsuta</i> | - | - | - | 1 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Erophila verna</i> | - | - | - | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Geranium pusillum</i> | - | - | - | 1 | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Helianthemum nummularium</i> | - | - | 1 | 2 | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Medicago lupulina</i> | - | - | 1 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Myosotis stricta</i> | - | - | - | 3 | - | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| <i>Phleum bertolonii</i> | - | - | - | 1 | - | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| <i>Ranunculus bulbosus</i> | - | - | 1 | 1 | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Saxifraga tridactylites</i> | - | - | 1 | - | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sedum album</i> | - | - | - | 2 | - | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Viola canina</i> | - | - | 1 | - | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| Total | 36 | 30 | 39 | 45 | 26 | 29 | | | | | | |

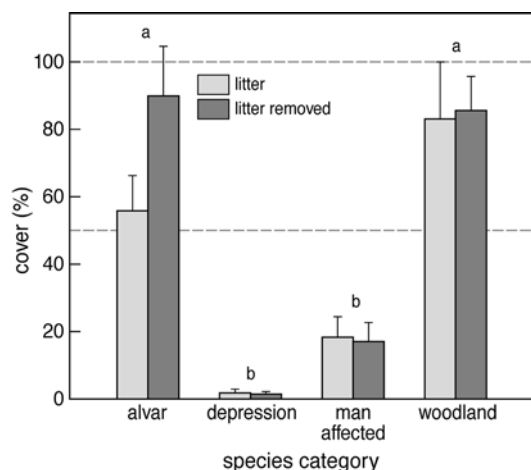


Fig. 1. Cover percentage of alvar, depression, man-affected and woodland species in the two treatments in 2008, after clearance in 1994 (mean + SE, $n = 4$, different letters indicate significant differences between species categories at $p < 0.001$; differences between litter treatments n.s.).

man-affected species forming a group of very low cover, there were no significant differences between the two litter removal treatments for any of the species categories (Fig. 1, univariate GLM species category: $F_{3,32} = 33.10$, $p < 0.001$, litter treatment: $F_{1,32} = 1.59$, n.s.).

Establishment and fate of alvar species after clearing

Irrespective of plots and treatments, 48 alvar species were found in the established vegetation during the 14-year observation period after clearing in 1994. The species pool under the dense scrub found in 1994 amounted to 49 species, including species in the established vegetation and soil seed bank. We classified the species found in one or both treatments in 1995 or 2008 into four groups. The first group includes 17 species present in both the established vegetation and soil seed bank under the dense scrub in 1994 (Table 1). Only *Poa compressa* was not found in the vegetation after clearance. The second group harbours 19 species present only in the established vegetation under the dense scrub in 1994. Six species of this group (e.g. *Danthonia decumbens*) did not establish themselves after

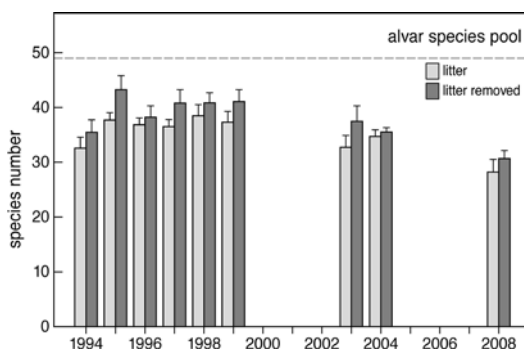


Fig. 2. Number of alvar species per plot of 2 × 2 m (mean + SE, $n = 4$) in the two treatments after scrub clearance in April 1994. The number of alvar grassland species is consistently and significantly higher in plots with the litter removal treatment (univariate GLM, litter treatment: $F_{1,72} = 12.26$, $p < 0.01$; year: $F_{1,72} = 25.06$, $p < 0.001$; replicate $F_{3,63} = 3.75$, $p < 0.05$). The alvar dry grassland species pool is indicated.

clearance. The third group harbours 13 species present only in the soil seed bank under the dense scrub in 1994. Four species of the group (e.g. *Centaurea scabiosa*) did not establish themselves one year after clearance, and most species disappeared 14 years after clearance; only four species maintained their presence. The fourth group includes 11 species found neither in the established vegetation nor in the soil seed bank under the dense scrub in 1994. They all appeared one year after clearance, but only four were still present 14 years after clearance, and only where the litter was removed.

The number of alvar species was about 35, of woodland species about 10, and of species of depressions and habitats strongly affected by man 2–3 (unpubl. data). Hence, we further discuss the results for the alvar species, which are also the target species after clearing. The average number of alvar grassland species (0.4 per m²) fluctuated during the study period in both litter treatments (Fig. 2). The number of alvar grassland species was consistently and significantly higher in plots where the litter was removed (univariate GLM, litter treatment: $F_{1,72} = 12.26$, $p < 0.01$; year: $F_{1,72} = 25.06$, $p < 0.001$; replicate $F_{3,63} = 3.75$, $p < 0.05$).

Ten species found in 1995 disappeared from the plots in 2008. Five established themselves

from the soil seed bank, namely, *Anthyllis vulneraria*, *Arenaria serpyllifolia*, *Polygala vulgaris*, *Sedum acre*, and *Trifolium campestre*. Two established themselves from vegetative parts (*Carex caryophylllea*, *C. ericetorum*), and three from either seeds or vegetative parts, or both (*Hieracium pilosella*, *Luzula campestris*, *Taraxacum* sp.). Most of the species that maintained their presence after establishment could spread from vegetative parts or from the soil seed bank. The four species that were found in more plots in 2008 than in 1995 all spread from vegetative parts: *Phleum phleoides*, *Primula veris* (target alvar grassland species), *Plantago lanceolata* and *Dactylis glomerata* (Table 1).

There was no significant difference in the dispersal traits, soil seed bank, seed weight, long-distance dispersal by wind, dung or fur of animals of 48 established and 11 non-established species (logistic regression, n.s.).

Discussion

Most of the species belonging to the community pool of dry alvar grassland species before clearance were found in the permanent plots between 2 and 14 years after the clearance. Our hypothesis that part of the characteristic alvar species could emerge from the persistent soil seed bank was confirmed. Species with a transient seed bank also established themselves, but they originated from vegetative spread from already existing vegetation. Removal of the litter and mosses did significantly and positively affect the re-establishment of alvar species. Hence, our second hypothesis that more alvar species would emerge after the removal of the litter and moss layer was confirmed. The group of *Agrostis capillaris* had species in the established vegetation and soil seed bank. Hence, these species can establish themselves from both sources. Of the group of *Agrostis vinealis* (only present in established vegetation) 13 species reappeared. Of the group of *Anthyllis vulneraria* (only present in the soil seed bank) four species reappeared (Table 1). Hence, only a small part of the long-term persistent soil seed bank resulted in the re-establishment of alvar species. The majority originated from vegetative spread from the

established vegetation. Which ecological mechanisms can explain these results?

The role of the community species pool

In the 1980s, this juniper scrub area was much more open than today. Via several paths it was easy for man and animals to visit open glades inside the today's very dense bush area. Our experimental plots were for practical reasons established just near such glades. It is very likely that several plant species survived near the paths as remnants of the formerly more open landscape. Animals might have brought seeds into the study area until some ten years ago. Today, transport from outside by birds and solitary grazers might be rather accidental.

The dense juniper scrub around the experimental plots makes seed dispersal from the open alvar grassland unlikely. Hence, we suppose that the re-establishment of alvar species must have taken place from the community species pool (Zobel *et al.* 1998) i.e. the soil seed bank, or through vegetative spread of the established vegetation. The community pool of alvar species under the junipers 80 years after abandonment amounted to 49 species (Table 1). The majority of the species in this dry alvar species pool (89%) were found after clearance in one of the years 1994–2008. Nine species (e.g. *Arenaria serpyllifolia*, *Linum catharticum*, *Polygala vulgaris*) were found only in the below-ground species pool before the clearance. In an earlier study (Bakker *et al.* 1996), they were classified as long-term persistent. Sixteen species found were present in both the established vegetation and the below-ground species pool prior to the clearance. Hence, they can either have emerged from existing vegetative parts (e.g. species with transient or short-term persistent seed bank such as *Briza media*, *Campanula persicifolia*, *Hieracium pilosella*), from seeds (e.g. species with long-term persistent seed bank such as *Luzula campestris*, *Potentilla tabernaemontani*) or from both (e.g. *Cerastium fontanum*, *Avenula pratensis*). Thirteen species were already present in the established vegetation before clearance (e.g. *Asperula tinctora*, *Filipendula vulgaris*, *Orchis mascula*). In an earlier study (Bakker *et al.* 1996),

these were classified as having a transient seed bank.

Clonal formations appeared gradually in the plots, subsequently taking over more and more space, thus outcompeting smaller species. Patches of grasses and *Fragaria viridis* are examples of that increase.

Removal of litter and mosses

Our long-term experiment (14 years after clearing) revealed clear differences between treatments: removal of litter and mosses did make a positive difference. This is in line with studies in which better seedling emergence and early establishment was found after removal of mosses and/or litter as compared with controls in dry grasslands (Van Tooren 1990, Jeschke & Kiehl 2008), flood meadows (Hölzel 2005) and moist fen meadows (Stammel *et al.* 2006). However, all these studies were short-term, i.e. up to three years.

In a greenhouse experiment, the alvar species *Arenaria serpyllifolia*, *Filipendula vulgaris* and *Veronica spicata* showed less seedling emergence when sown in moss carpet or lichen clumps than on bare soil, whereas *Festuca ovina* showed no differences (Zamfir 2000). The moss layer may form a mechanical barrier and prevent seeds from reaching the soil (Van Tooren 1988, Jeschke & Kiehl 2008). The moss layer may also diminish the amount of light reaching the soil and the red/far-red ratio in the transmitted light with negative effects on seedling establishment (Jensen & Gutkunst 2003). However, a thick moss layer may create a humid microclimate (Van Tooren 1988) with subsequent positive effects on seedling establishment (Keizer *et al.* 1985). Our experiment with the removal of litter and mosses by raking created an area of bare soil of several square metres thus creating harsh conditions during the warm summer period when there is little precipitation on Öland (Rosén 1982). Jeschke and Kiehl (2008) reported high seedling mortality during dry periods in the summer. Kiefer and Poschod (1996) suggested that several species could not establish themselves after clearing as a result of heavy water stress and strong frost at the cleared site. We assume that frost might have

had a negative effect on some species, especially where the litter was removed. In the same areas, the drought probably killed several plants during extreme conditions especially during May–July 1999 and 2002 with respectively only 30 and 7 mm of rain (data from the Station Linné on Öland). Our experiment revealed that more alvar species were re-established after the moss and litter layers were removed by raking than when these layers were left untouched. Apparently the advantages of removal of the moss and litter layers overrode the disadvantages.

It should, however, be considered that with both litter removal and leaving the litter, a decline in species number was found. We suppose that the rapid resprouting of *Rosa canina* and *Prunus spinosa* caused light attenuation.

Species traits

Species traits, such as seed weight, interact with the effects of the layer of mosses and litter. Germination and seedling establishment of heavy seeds is less hampered by the litter layer than those of light seeds (Grime & Jeffrey 1965, Leishman & Westoby 1994, Jensen & Gutkunst 2003, Hölzel 2005, Stammel *et al.* 2006). When it comes to re-establishment of alvar species after a long period of abandonment, large-seeded species seem to have an advantage over small-seeded species. The problem is that alvar species with transient or short-term persistent seed bank have larger seeds than those with a long-term persistent seed bank (Bakker *et al.* 1996). Thus the species that are best adapted to germination and seedling establishment under a layer of mosses and litter already disappeared from the soil seed bank when the clearing takes place. The species that are still present in the soil seed bank are less well adapted to the new conditions offered by the clearing. Hence, it is likely that the species which re-establish or spread after clearing do so from still existing vegetative parts. Pärtel *et al.* (1998) found that none of the alvar species disappeared completely from the local species pool after abandonment.

The fact that no significant differences were found in dispersal traits of the 48 established species after clearance and the 11 non-established

species indicates that the species composition of the restored sites is a representative set of the community species pool when considering dispersal traits. Of the species pool of 49 alvar species, only four have the potential to be wind-dispersed (Table 1). Moreover, it is unlikely that they could disperse into the experimental plots which were surrounded by a dense juniper scrub. However, 16 species have the potential to travel by fur, and 26 by dung of animals. The fact that the cleared site was surrounded by a dense juniper scrub prevented livestock from dispersing seeds. Thus long-distance dispersal did not play a role in the emergence of species after clearing. The species with a persistent seed bank were still present and could germinate after clearing. The species with a transient seed bank could not emerge from seeds, but did emerge through vegetative spreading, and could do so without long-distance dispersal. The cutting of junipers, and thus connecting the cleared site with the surrounding alvar, should allow for long-distance dispersal by livestock. This result was found after cutting trees, and subsequent grazing by sheep of overgrown calcareous grasslands (Poschlod *et al.* 2002).

Conservation issues

In the absence of grazing, the tall canopy may in the long run be the reason for a decrease in species numbers due to light attenuation. Our suggestions for management of alvar overgrown by juniper scrub include cutting of the shrubs. Cut junipers do not resprout easily. However, rapidly sprouting species, such as *Rosa canina* and *Prunus spinosa*, should be managed. Removal of individuals or small groups of shrubs provides sufficient access for alvar species, including those with a transient seed bank (Bakker *et al.* 2007). Removal of litter and mosses will benefit the re-establishment of alvar grassland species. In a dense scrub openings to the surrounding open alvar are needed to promote dispersal of alvar species by wind and livestock. Again, large-scale removal of litter and mosses is not feasible while small-scale removal may benefit the re-establishment of alvar grassland species. It may be better to have livestock creating small-scale gaps by trampling.

Acknowledgements

We thank the staff of the Station Linné at Öland for support. We acknowledge the help of Geurt Verweij and Liesbeth Bakker in establishing the experiment in 1994. Moreover, we acknowledge the help of students of the Community Ecological Research Course 2008 of the Universities of Groningen and Oldenburg for their help during fieldwork. We appreciate the useful comments from two reviewers.

References

- Bakker, J. P., Bakker, E. S., Rosén, E., Bekker, R. M. & Verweij, G. L. 1996: The soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* scrubland. — *Journal of Vegetation Science* 7: 165–176.
- Bakker, J. P., Rosén, E. & Steg, K. 2007: Re-establishment of alvar plant species in abandoned arable fields on Öland. — *Acta Phytogeographica Suecica* 88: 73–82.
- Bengtsson, K., Prentice, H., Rosén, E., Moberg, R. & Sjögren, E. 1988: The dry alvar grasslands of Öland: ecological amplitudes of plant species in relation to vegetation composition. — *Acta Phytogeographica Suecica* 76: 21–46.
- Grime, J. P. & Jeffrey, D. W. 1965: Seedling establishment in vertical gradients of sunlight. — *Journal of Ecology* 53: 621–642.
- Hölzel, N. 2005: Seedling recruitment in flood-meadow species: The effects of gaps, litter and vegetation matrix. — *Applied Vegetation Science* 8: 115–124.
- Jensen, K. & Gutekunst, K. 2003: Effects of litter on establishment of grassland plant species: the role of seed size and successional status. — *Basic and Applied Ecology* 6: 579–587.
- Jeschke, M. & Kiehl, K. 2008: Effects of a dense moss layer on germination and establishment of vascular plants in newly created calcareous grasslands. — *Flora* 203: 557–566.
- Kalamees, R. & Zobel, M. 1997: The seed bank in an Estonian calcareous grassland: comparison of different successional stages. — *Folia Geobotanica Phytotaxonomica* 32: 1–14.
- Keizer, P. J., Van Tooren, B. F. & Duuring, H. J. 1985: Effects of bryophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. — *Journal of Ecology* 73: 493–504.
- Kiefer, S. & Poschlod, P. 1996: Restoration of fallow of afforested calcareous grasslands by clear-cutting. — In: Settele, J., Margules, C. R., Poschlod, P. & Henle, K. (eds), *Species survival in fragmented landscapes*: 209–218. Kluwer, Dordrecht.
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Endels, P., Götzenberger, L., Hodgson, J., Jackel, A. K., Dannemann, A., Kühn, I., Kunzmann, D., Ozinga, W. A., Römermann, C., Stadler, M., Schlegel-

- milch, J., Steendam, H., Tackenberg, O., Wilmann, B., Cornelissen, J. H. C., Eriksson, O., Garnier, E. & Peco, B. 2008: The LEDA Traitbase: a database of life-history traits of the northwest European flora. — *Journal of Ecology* 96: 1266–1274.
- Knevel, I. C., Bekker, R. M., Kleyer, M. & Bakker, J. P. 2003: Life-history traits of the northwest European flora: a database (LEDA). — *Journal of Vegetation Science* 14: 611–614.
- Königsson, L.-K. 1968: The Holocene history of the Great Alvar of Öland. — *Acta Phytogeographica Suecica* 55: 1–172.
- Leishman, M. R. & Westoby, M. 1994: The role of large seed size in shaded conditions: experimental evidence. — *Functional Ecology* 8: 205–214.
- Londo, G. 1976: The decimal scale for relevés of permanent plots. — *Vegetatio* 33: 61–64.
- Lid, J. 1987: *Norsk, Svensk, Finsk Flora*. — Det Norske Samlaget, Oslo.
- Ozinga, W. A., Bekker, R. M., Schaminée, J. H. J. & Van Groenendael, J. M. 2004: Dispersal potential in plant communities depends on environmental conditions. — *Journal of Ecology* 92: 767–777.
- Ozinga, W. A., Römermann, C., Bekker, R. M., Tamis, W. L. M., Prinzing, A., Schaminée, J. H. J., Hennekens, S., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J. P. & Van Groenendael, J. M. 2009: Dispersal failure contributes to plant losses in NW Europe. — *Ecology Letters* 12: 66–74.
- Pakeman, R., Digneffe, G. & Small, J. L. 2002: Ecological correlates of endozoochory by herbivores. — *Functional Ecology* 16: 296–304.
- Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. 1998: Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. — *Ecological Engineering* 10: 275–286.
- Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. 1999: Alvar grasslands in Estonia: variation in species composition and community structure. — *Journal of Vegetation Science* 10: 561–570.
- Poschlod, P., Kiefer, S., Tränkle, U., Fischer, S. & Bonn, S. 2002: Plants species richness in calcareous grasslands as affected by dispersability in space and time. — *Applied Vegetation Science* 1: 75–90.
- Rejmánek, M. & Rosén, E. 1988: The effects of colonizing shrubs (*Juniperis communis* and *Potentilla fruticosa*) on species richness in the grasslands of Stora Alvaret, Öland (Sweden). — *Acta Phytogeographica Suecica* 76: 67–72.
- Rejmánek, M. & Rosén, E. 1992: Influence of colonising shrubs on species area relationships in alvar plant communities. — *Journal of Vegetation Science* 3: 625–630.
- Rosén, E. 1982: Vegetation development and sheep grazing in limestone grasslands of south Öland. — *Acta Phytogeographica Suecica* 72: 1–172.
- Rosén, E. 1988: Shrub expansion in alvar grasslands on Öland. — *Acta Phytogeographica Suecica* 76: 87–100.
- Rosén, E. & Sjögren, E. 1988: Plant cover in alvar junipers on Öland. Distribution features correlated to shrub size and shape. — *Acta Phytogeographica Suecica* 76: 101–112.
- Rosén, E. & Van der Maarel, E. 2000: Restoration of alvar vegetation on Öland, Sweden. — *Applied Vegetation Science* 3: 65–72.
- Schaefer, C. A. & Larson, D. W. 1997: Vegetation, environmental characteristics and ideas on maintenance of alvars on the Bruce Peninsula, Canada. — *Journal of Vegetation Science* 8: 797–810.
- Stammel, B., Kiehl, K. & Pfadenhauer, J. 2006: Effects of experimental and real land use on seedling recruitment of six fen species. — *Basic and Applied Ecology* 7: 334–346.
- Van der Maarel, E. 1988: Floristic diversity and guild structure in the grasslands of Öland's Stora Alvaret. — *Acta Phytogeographica Suecica* 76: 53–76.
- Van der Maarel, E. & Sykes, M. T. 1993: Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. — *Journal of Vegetation Science* 4: 179–188.
- Van Tooren, B. F. 1988: The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. — *Oikos* 53: 41–48.
- Van Tooren, B. F. 1990: Effects of a bryophyte layer on the emergence of seedlings of chalk grassland species. — *Acta Oecologia* 11: 155–163.
- Zamfir, M. 2000: Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. — *Oikos* 88: 603–611.
- Zobel, M., Van der Maarel, E. & Dupré, C. 1998: Species pool: the concept, its determination and significance for community restoration. — *Applied Vegetation Science* 1: 55–66.
- Znamenskiy, S., Helm, A. & Pärtel, M. 2006: Threatened alvar grasslands in NW Russia and their relationship to alvars in Estonia. — *Biodiversity and Conservation* 15: 1797–1809.